

## EFFECTS OF ENVIRONMENTAL AND SPATIAL FEATURES ON MUSSEL POPULATIONS AND COMMUNITIES IN A NORTH AMERICAN RIVER

Barry P. Baldigo<sup>1</sup>, Karen Riva-Murray<sup>1</sup> and George E. Schuler<sup>2</sup>

### ABSTRACT

Decreases in mussel-species richness and their distributions in rivers worldwide may indicate these long-lived organisms are adversely affected by recent changes in suitability of habitat and (or) quality of surface waters. Unionid mussel communities and local physical-habitat and water-quality conditions were determined across the Neversink River in southeastern New York State to evaluate factors that affect the distribution and abundance of common and rare mussel species and the richness of mussel communities. Results from correlation and partial regression analyses indicate: (1) macrohabitat features such as percent open canopy, mean channel width, mean bank width, several water-quality factors (e.g., conductivity and pH), and reach physiography (e.g., elevation and drainage area) affected mussel-community richness and the distribution of *Alasmidonta heterodon* (Lea 1829) populations; and (2) the abandoned, low-head Cuddebackville Dam may have restricted *A. heterodon* populations to the lower reaches of the system. Potential positive affects of the main stem reservoir and negative effects of the abandoned dam on mussel populations indicate that the response of intended targets need to be well understood for effective management of impoundments, downstream flows, and biological resources in rivers of the world.

Keywords: Habitat, *Alasmidonta heterodon*, *A. varicosa*, *A. undulata*, *Anodonta implicata*, *Elliptio complanata*, *Pyganodon cataracta*, *Strophitus undulatus*, mussel, community, richness, reservoir, impoundment, dam, Neversink.

### INTRODUCTION

Freshwater mussels (Unionidae) are some of the most imperiled fauna in North America – from 43 to 72% of the native species have been classified as extinct, endangered, threatened, or vulnerable (Bogan, 1993; Master, 1990; Williams & Neves, 1995). Decreases in mussel-species richness and their distributions worldwide indicate that these long-lived organisms have been adversely affected by alterations in habitat suitability, water quality, and the spread of non-indigenous species (Williams *et al.*, 1993). Although impoundments and associated changes in water quality, local fish populations, and temperature, flow, and sediment regimes contribute to these declines (Brim-Box & Mossa 1999; Vaughn & Taylor, 1999; Williams & Neves, 1995), specific factors and

<sup>1</sup>U.S. Geological Survey, Water Resources Division, 425 Jordan Road, Troy, NY 12180, U.S.A. E-mail: [bbaldigo@usgs.gov](mailto:bbaldigo@usgs.gov); telephone: (518) 285-5605; [krmurray@usgs.gov](mailto:krmurray@usgs.gov); (518) 285-5617.

<sup>2</sup>The Nature Conservancy, Neversink River Preserve, P.O. Box 617, Cuddebackville, NY 12729, U.S.A. E-mail: [gschuler@warwick.net](mailto:gschuler@warwick.net); telephone: (845) 858-2883.

processes that affect abundance of mussel populations and the distribution of mussel species are poorly understood (Strayer, 1983; Strayer & Ralley, 1993). A number of studies have shown or proposed that certain microhabitat conditions can restrict mussel species to isolated patches in rivers. For example, Strayer & Ralley (1993) and others (Layzer & Madison, 1995; Strayer, 1993; Strayer & Ralley, 1991) determined that shear stress, water velocity, substrate particle sizes, and sediment stability might affect the presence or absence of certain species and richness of mussel species in riverine systems. The effects that large-scale, macrohabitat factors have on mussel-species populations, however, are poorly defined. In this report, "microhabitat" refers to environmental factors that potentially affect mussel species at the location of an individual specimen and are generally on a scale of one meter or less, and "macrohabitat" refers to physical and chemical factors that potentially affect species populations at the reach scale of 10's to 100's of meters. Macrohabitat also includes physiographic factors measured at the landscape or watershed scale, such as elevation, discharge, and drainage area, which may function as surrogates for overall habitat condition at the reach level. Macrohabitat features appear to determine suitability of a river reach for certain species; whereas, correlated or unrelated microhabitat factors limit where stable mussel beds (patches) may become established and sustained within suitable reaches. Many mussel species are also long-lived and propagate using various host-specific fish species (Strayer & Jirka, 1997). Patterns and variation in mussel-species distributions, abundance of species populations, and mussel communities, therefore, may be determined by a multitude of biotic, historical, and landscape-level constraints as well as local physical and chemical (environmental) conditions (Vaughn & Taylor, 2000).

Spatial autocorrelation and multi-correlation among predictor variables are issues particularly difficult to overcome when attempting to define relations in any observational study. Many environmental features and the distribution and abundance of aquatic species generally display strong spatial structure in a river system which can obscure, or more likely inflate, relations between ecological patterns and constraining/predictor variables. In addition, many predictor variables in rivers typically reflect various degrees of multi-correlation, and could be interdependent. Thus, the response gradient for selected aquatic community or population indices or measures might be misinterpreted simply due to the spatial structure of processes operating at different scales across sampled locations. Fortunately, the effects of different components on dependent variables can be partly isolated and separated into variation explained by pure spatial and environmental components and variation shared between and among components using partial regression analyses (Legendre & Legendre, 1998). It

must be stressed that associations defined herein do not reflect cause and effect relations, but provide a foundation for further exploration of the factors that affect the health and distribution of mussel-species populations.

The Neversink River in southeastern New York State (Fig. 1) and extant mussel-species populations are unique in a number of respects and provide a good opportunity to assess factors that may affect the health and distribution of resident mussel species and communities. The basin supports two main stem dams, one large active reservoir for municipal supplies in the upper/middle basin and one low-head abandoned structure in the lower basin (Fig. 1). Concentrations of dissolved minerals and salts in the basin are low and may approach lower limits for proper shell accretion in certain species (Strayer & Jirka, 1997). The system also possesses the richest diversity of freshwater mussels in the upper Delaware River Basin (Strayer & Ralley, 1991). One of the seven mussel species that occur in the Neversink is federally endangered, and another is on the draft New York State threatened-species list (The Nature Conservatory [TNC], 1949). Populations of the endangered dwarf wedgemussel (*Alasmidonta heterodon* Lea 1829) are restricted to a 18-km section in the lower third of the basin, whereas the threatened swollen wedgemussels (*Alasmidonta varicosa* Lamarck 1819) occupy the lower half of the basin (Strayer & Ralley, 1991; Strayer *et al.*, 1996). Dwarf wedgemussels have been collected only downstream from the abandoned, low-head Cuddebackville Dam (Fig. 1) (Strayer & Ralley, 1991; TNC, 1999). This population is one of the largest in the Northeast, but its limited distribution suggests it may be susceptible to local extinctions due to catastrophic floods, localized fuel or chemical spills, or epidemic diseases. Protecting and promoting *A. heterodon* populations in the Neversink Basin is problematic because: (1) they occur in beds that are patchily distributed which make distributions difficult to quantify, (2) the abandoned Cuddebackville Dam may restrict upstream movement of their host fish and, thus, the distribution of *A. heterodon* populations, and (3) the relationship of environmental factors to the distribution and abundance of their populations are poorly understood (Strayer, 1993; Strayer & Ralley, 1993; Strayer *et al.*, 1996; TNC, 1995).

The main objective of this paper is to identify the factors that potentially govern the distribution of mussel-species populations in the Neversink River Basin. This is achieved by assessing the importance of chemical and physical features on mussel-community richness and abundance and on the relative abundance of species populations in the basin. Related objectives are to: (1) characterize the range of endangered and threatened species in the basin, (2) evaluate the potential effects of the Cuddebackville Dam on rare-species populations, and (3) rank the influence of specific physical and chemical factors

on mussel communities and the distribution of species populations across the basin.

#### FIELD-SITE DESCRIPTION

The Neversink River drains about 1126 km<sup>2</sup> of land and forms headwaters for the Delaware River Basin. The river flows through four distinct physiographic regions. The 238-km<sup>2</sup> upper Neversink sub-basin is mountainous and terminates at the Neversink Reservoir and Dam. The 606 km<sup>2</sup> middle Neversink sub-basin, located between the reservoir and the confluence with the Basha Kill, starts as a broad floodplain but passes through a narrow gorge for most of its length. The 93-km<sup>2</sup> lower Neversink sub-basin is a broad river with an ancient, relatively narrow floodplain. The 189 km<sup>2</sup> Basha Kill sub-basin is the largest tributary to the lower Neversink and consists of a 12-km<sup>2</sup> stillwater marsh and several small tributaries. Its watershed is relatively undeveloped with only one city, Monticello, totally within the drainage basin.

The Neversink Reservoir and the Cuddebackville Dam potentially affect water quality, hydrology, habitat, and biological communities in the main-stem of the Neversink River. The reservoir is in the upper basin, covers 6.1 km<sup>2</sup> in surface area, and impounds 132,500,000 m<sup>3</sup> of water. During the 1997 water year, the reservoir released an average of 1.1 cubic meters of water per second (cms) into the Neversink (average daily flows varied from 0.7 to 2.0 cms depending on season) at a USGS gage immediately downstream of the dam, with an additional 6.2 cms diverted continuously to the New York City water-supply system (Butch *et al.*, 1998; Krejmas *et al.*, 1998). The annual mean discharge at the gage fell from 7.5 cms to just over 1.4 cms, the average length of low pulses increased from 6 to 44 days, and the average length of high pulses dropped from 5.3 to 2.7 after impoundment (TNC, 1999). The low-head Cuddebackville Dam is located on the main-stem Neversink River, about 2.5 km upstream from its confluence with the Basha Kill. It was first constructed in the early 1800s, rebuilt several times, and abandoned in the middle 1900s. The dam is currently in disrepair, has a 2-m high waterfall, confines a relatively small amount of sediment and standing water, and blocks upstream movement of several resident and anadromous fish species.

#### METHODS

Methods for mussel, water-quality, and habitat sampling and analysis and for statistical analyses are summarized below. Overall, 28 reaches on the main-stem and tributaries of the Neversink River were selected for study. Not all reaches were inventoried for mussels or for physical-habitat features because of resource limitations. Reach locations, names, and identifier codes are shown in Fig. 1.

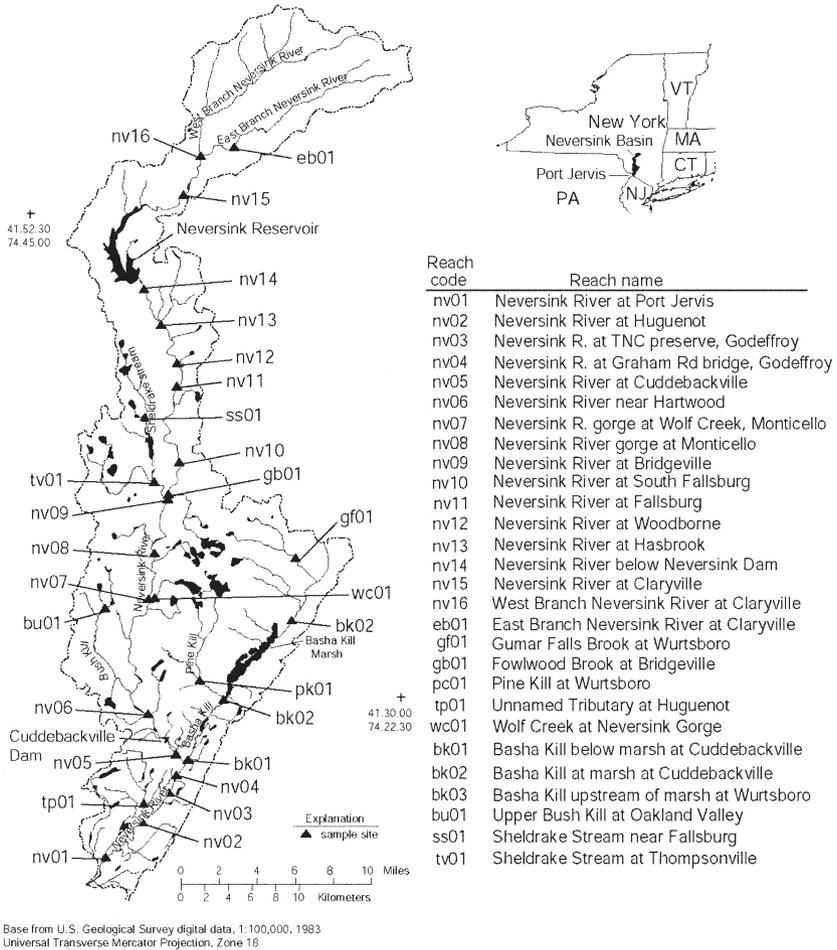


FIG. 1. Location and names for 28 reaches studied in the Neversink River Basin in southeastern New York State, 1997-2001.

*Mussel-species surveys*

Mussel searches were conducted during June 1997 at 25 reaches from which previous mussel data were not available. Mussel data for three reaches were obtained from semi-quantitative surveys done between 1994 and 1997 (written communication, D.L. Strayer, Feb., 1998). At each reach, two people searched for mussels along a 100- to 400-meter long reach for a total of 1 h using a combination of snorkeling and (or) wading with a view tube. Searches were extended to 2 hr if mussels were found during the first hour. Once a mussel bed was located, it was searched intensively, and all individuals found were identified, counted, and returned to the same area. A recent investigation of sampling efficiencies for timed mussel searches (Metcalf-Smith *et al.*,

2000) showed that more rare species could be found if search times were at least 4.5 person hours per reach. Though longer searches were not feasible for the present study, a 2-hr search period produces catch rates that have been correlated with species density and proven to be reliable estimates of species richness (Strayer *et al.*, 1997). Relative abundance or density for: (1) the total number of mussels, and (2) number of each species for each reach were estimated as a catch rate (the number observed divided by the number of person hours searched). Most abundance data were rescaled to the number observed per 10-hours for statistical analyses to eliminate negative values when fractional data were  $\log_{10}$ -transformed.

#### *Water quality*

Water samples were collected from all 26 reaches, once in September 2000 and again in April 2001. Reaches nv08 and nv09 were sampled once in August 1997, but not during the later period due to access limitations. Monthly samples were collected between March 2000 and April 2001 at nv01, nv04, bk01, nv05, and nv12. Stream-water temperatures were measured when samples were collected. Samples were collected from a well-mixed section of the channel, placed on ice, and transported to the U.S. Geological Survey (USGS) laboratory in Troy, NY. Aliquots were filtered, preserved, shipped to the USGS National Water Quality Laboratory in Denver, CO, and analyzed for pH, conductivity, acid-neutralizing capacity (ANC), major cations and anions, and nutrients in accordance with standard USGS methods (Fishman & Friedman, 1989; Wolman, 1954). Dissolved organic carbon (DOC) concentrations were measured at the USGS Laboratory in Troy, NY, following standard methods (Lawrence *et al.*, 1995).

#### *Habitat*

Habitat and hydraulic characteristics were characterized at 20 reaches during June-July 1997, when discharge was at or near base flow. Habitat was not surveyed at reaches eb01, gf01, gb01, pc01, bk03, wc01, nv14, and tp01. Selected channel-morphology, substrate-particle size, bank stability, riparian vegetation, and hydraulic characters included those that describe physical stream habitat at reach and pool/riffle scales (Frissell *et al.*, 1986) and have been hypothesized to affect the abundance of mussels or community richness (Layzer & Madison, 1995; Michaelson & Neves, 1995; Strayer *et al.*, 1996; Strayer, 1993; Strayer & Ralley, 1993). Habitat-survey reaches bounded local mussel beds or search areas and were typically 20 mean-stream widths (MSW) in length (Meador *et al.*, 1993; Simonson *et al.*, 1993; Simonson *et al.*, 1994), but no longer than a predetermined 300-m maximum. The length of each geomorphic channel unit (pool, riffle, run) was measured according the methods summarized in Meador *et al.* (1993). In-stream channel features and bank conditions were measured or visually estimated at 5-7 transects spaced 1-2 MSW apart, depending on stream width. Transect spacing was one MSW in streams greater than 10 m wide and two MSWs in streams less than 10 m wide.

Measurements of channel depth and substrate types, water velocity, and estimates of percent algal and macrophyte cover, were made at five or seven equally spaced points across each transect and at the thalweg. Measurements were generally made at five points in channels less than 20 m wide, and at seven points in channels greater than 20 m wide. Water depth was measured to the nearest cm, velocity was measured at six-tenths depth with a mechanical or electromagnetic water-velocity meter, and depth of fine sediments was measured according to methods described in Simonson *et al.*, (1994). Substrate sizes for the reach were quantified by modified Wolman-count methods (Wolman, 1954), in which five particles were randomly selected near each transect point, and the intermediate particle lengths recorded. Embeddedness was estimated to the nearest 5% (Platts *et al.*, 1983) for three gravel or larger-sized particles at each point.

Bank and riparian characteristics, unless otherwise noted, were measured or visually estimated

at both ends of each transect according to methods described in Meador *et al.* (1993). Angle of open canopy was estimated with a climometer at the midpoint of each transect. Bankfull width and height, and total wetted width were measured for each transect according to methods of Simonson *et al.* (1994). Indicators of recurring high flows, such as debris dams, erosion lines, and vegetated extent, were used to estimate top or landward edge of the bank (generally bankfull). The streamward edge of the bank was defined as the edge of water. Bank shape was characterized as linear, concave, or convex. The percent of vegetated bank cover and type (trees, shrubs, grasses, or bare), angle of inclination, substrate types, and degree of erosion were estimated at both ends of each transect. Various land-use classes, and the percentage of each on both banks, were visually estimated from edge of water to 50 m away from the bank. Discharge at each reach was calculated as the average of flows at all transect; transect flows were determined from point velocities, depths, and widths of transect segments using modified USGS methods (Rantz, 1983). Elevation, stream-channel gradient, and watershed drainage area for each reach were determined from 1:24,000 scale USGS maps.

### *Statistical analyses*

The effects of physical, chemical, and spatial factors and the Cuddebackville Dam on mussel-species assemblages were evaluated at 20 reaches where habitat was surveyed, using correlation and simple linear and partial multiple regression techniques (Legendre & Legendre, 1998). Mean, minimum, maximum, or total (cumulative) physical-habitat variables, elevation, and drainage area (treated as physical characters), and median estimates of each chemical parameter were used as predictor variables. Most physical-habitat and chemical data were  $\log_{10}$  transformed to improve normality of their distributions. The number of mussel species, total abundance, and species abundance data were increased by 1 before being  $\log_{10}$  transformed to avoid invalid data and omission from subsequent analyses. For all analyses, the numbers of physical and chemical variables were initially reduced using Principal Components Analyses (PCA) to isolate variables strongly correlated with major physical-habitat or chemical gradients. Important principal-component axes were used in regression analyses as pseudo-variables when they accounted for large amounts of variation in dependent mussel variables. Multi-correlated variables were identified and the total number of variables further reduced using both PCA and correlation analyses. The distance of each reach from the confluence of the Neversink and Delaware was used to define each reach's location and the spatial structure in this system because spatial orientation was nearly linear for the 20 main stem reaches. A binary-dummy variable described the spatial orientation of each reach either upstream (1) or downstream (0) from the Cuddebackville Dam and was used to assess its affect on dependent-mussel variables.

Partial regression analyses used mussel-species richness, total abundance of all mussels, and abundance of each mussel species as dependent variables, and partitioned variation into that explained by chemical, physical, or spatial components. For analysis of each dependent variable (*e.g.*, mussel richness), we first determined the variation explained by physical-habitat, chemical, and spatial components (sets of variables) alone, through a forward-selection process (Legendre & Legendre, 1998). Variables were retained that significantly ( $p \leq 0.10$ ) explained the largest amount of variation remaining in dependent variables after earlier selections. The sets of physical, chemical, and spatial variables that were significantly related to each dependent variable alone were then used in various combinations (chemical and physical; chemical and spatial; physical and spatial; and chemical, physical, and spatial), regardless of statistical significance of slope coefficients, to determine the total variation explained/unexplained and the proportion of shared variation (overlap) between and among the three components. The proportion of variation in dependent variables explained by pure physical-habitat (P), pure chemical (C), and pure spatial (S) components; shared among physical and spatial (P+S), physical and chemical (P+C), chemical and

TABLE 1. Selected physical, chemical, and spatial characteristics for 20 study reaches in the Neversink River Basin, NY. [Physical data are from surveys conducted June-July 1997; chemical data are from 2 to 14 samples collected March 2000-April 2001; site names and locations are given in Fig. 1.]

Study reach name	Watershed area (km <sup>2</sup> )	Elevation (m)	Mean annual flow (cms)	Mean channel slope (%)	Open canopy (%)	Mean channel width (m)	Mean channel depth (m)	Sand substrate (%)	Cobble substrate (%)	Mean particle size (mm)	Mean embeddedness (%)
bk01	178	159	6.00	0.10	24.2	15.7	44.7	32.7	28.7	45.3	43.5
bk02	156	155	5.23	0.10	15.1	7.7	16.8	8.4	55.5	79.0	31.9
bu01	14	464	0.46	0.30	20.7	6.9	28.0	45.0	27.8	45.7	56.8
nv01	844	109	12.93	0.09	44.4	42.9	79.6	88.6	0	3.6	na
nv02	826	143	12.59	0.11	34.4	45.3	52.7	16.0	31.4	48.4	41.7
nv03	798	146	12.08	0.36	35.8	42.3	73.2	17.1	62.3	86.5	29.2
nv04	794	151	11.99	0.39	46.3	54.3	46.0	11.5	71.5	130.2	31.4
nv05	614	149	8.60	0.33	43.1	34.1	36.1	10.3	61.1	142.9	41.3
nv06	591	187	8.18	0.70	53.8	39.2	26.4	2.4	54.1	194.4	19.1
nv07	480	298	6.08	0.74	44.4	29.1	52.8	11.2	15.9	2684.5	19.0
nv08	460	323	5.70	0.25	47.7	32.6	33.8	17.0	32.1	224.7	38.1
nv09	435	335	5.24	0.15	52.4	32.8	31.9	28.0	37.1	67.1	46.0
nv10	326	337	3.19	0.17	61.3	32.9	27.2	15.4	52.5	87.1	39.9
nv11	303	347	2.76	0.25	40.6	21.0	46.4	13.2	48.4	64.5	27.7
nv12	293	351	2.58	0.26	58.2	33.9	34.6	33.5	33.5	68.7	50.4
nv13	273	360	2.20	0.40	47.2	25.0	60.9	33.3	43.0	61.5	50.2
nv15	173	465	5.80	0.64	67.5	25.9	30.8	18.0	61.9	98.8	20.3
nv16	88	493	2.94	0.82	39.8	15.7	30.6	3.3	60.0	157.1	8.7
ss01	24	373	0.79	0.69	15.4	5.6	18.1	24.4	35.3	50.2	43.3
tv01	39	358	1.30	0.91	21.7	11.3	25.7	17.4	44.5	714.9	45.3

(continued on next page)

TABLE 1 (continued)

Study reach name	Watershed area (km <sup>2</sup> )	Elevation (m)	Mean annual flow (cms)	Mean channel slope (%)	Open canopy (%)	Mean channel width (m)	Mean channel depth (m)	Sand substrate (%)	Cobble substrate (%)	Mean particle size (mm)	Mean embeddedness (%)
bk01	32.2	9.89	6.95	23.0	3.90	0.004	0.259	0.089	0.004	0.013	15.9
bk02	28.0	8.35	7.00	20.0	2.35	0.002	0.194	0.022	0.003	0.054	16.6
bu01	13.4	4.05	6.95	6.5	1.75	0.013	0.244	0.018	0.002	0.013	33.5
nv01	26.2	8.00	7.05	17.0	3.25	0.010	0.507	0.317	0.017	0.028	3.3
nv02	24.0	7.40	7.15	16.5	2.85	0.002	0.400	0.256	0.011	0.026	9.0
nv03	23.8	7.42	6.90	16.0	2.70	0.004	0.433	0.277	0.013	0.026	12.5
nv04	23.8	7.24	6.95	15.0	3.05	0.009	0.626	0.381	0.020	0.043	14.2
nv05	20.5	6.17	7.05	12.0	2.85	0.01	0.576	0.391	0.03	0.052	16.5
nv06	17.0	5.13	7.15	10.5	2.35	0.004	0.542	0.353	0.027	0.044	21.2
nv07	17.5	5.24	7.05	9.5	2.25	0.005	0.660	0.500	0.038	0.056	34.1
nv08	na	4.14	7.00	5.7	1.97	na	na	na	na	na	38.6
nv09	na	5.49	7.32	10.5	1.78	na	na	na	na	na	44.5
nv10	13.2	3.86	6.85	6.5	2.30	0.011	0.598	0.436	0.039	0.022	48.1
nv11	11.4	3.30	6.90	6.0	2.15	0.007	0.428	0.271	0.003	0.008	56.6
nv12	13.0	3.77	6.9	6.5	2.55	0.010	0.437	0.316	0.004	0.008	59.0
nv13	10.8	3.09	7.05	5.5	2.25	0.074	0.467	0.293	0.002	0.006	63.5
nv15	7.9	2.20	7.10	3.5	2.20	0.003	0.319	0.237	0.002	0.004	81.7
nv16	8.6	2.56	-4.0	1.80	0.037	0.464	0.394	0.004	0.003	85.9	
ss01	28.1	8.63	7.15	18.5	2.00	0.010	1.196	0.831	0.053	0.084	53.5
tv01	33.3	10.28	6.95	17.0	2.20	0.010	1.126	0.737	0.028	0.056	46.9

<sup>1</sup> acid neutralizing capacity

<sup>2</sup> nitrogen

<sup>3</sup> phosphorus

spatial (C+S) components; shared among all three (P+C+S) components; and the total amounts of explained and unexplained variation were partitioned following addition and subtraction techniques described by Legendre & Legendre (1998), modified for three components. The variation attributed to spatial factors was further partitioned into that which could be explained by pure location (river kilometers), pure dam (binary), and variation shared by location and the dam using two-component partitioning techniques. The only deviation from the methods of Legendre & Legendre (1998) was the use of adjusted, rather than unadjusted regression coefficients, to more conservatively estimate amounts of variation in dependent variables explained when using multiple predictor variables.

Interpretations below may be contentious because our analyses were limited to a relatively small number of sites and interactions between predictor variables potentially confound true associations. Inferred relations, however, provide a basis for further exploration of the factors that affect the health and distribution of mussel-species populations.

## RESULTS

### *Reach characteristics*

Stream-reach elevation, drainage area, slope, and other selected characteristics at the 20 sites where habitat was assessed are provided in Table 1. With several exceptions, the sites reflected typical differences between low-order, high-elevation reaches with a small drainage area, steep slope, high water velocities, and cool temperatures, and high-order, low-elevation reaches with a large drainage area, low slope, low water velocities, and high temperatures. Several tributary reaches of low to middle order, such as bu01, bk01, and bk02 (Fig. 1) originated in marshes and were atypical stream reaches. Reaches nv13 and nv14, immediately below the Neversink Reservoir, and the lowest main-stem reach nv01 (Fig. 1), also exhibited many unique physical conditions related to their unusual flow, sediment, or thermal regimes. Three reaches (nv16, nv15, and eb01) in the upper basin, and reaches nv10, nv11, nv12, and nv14, below the Neversink Reservoir, showed some degree of acidification. High water temperatures (near 25°C) and low dissolved oxygen concentrations (4.5 mg/L) were observed at reaches nv01 and bk02. Low oxygen concentrations, stream slope, and water velocities and a deep layer of fine sediments indicate that nv01 was not a typical riverine reach.

### *Distribution of mussel species*

Mussel-species richness, total number collected per hour, and the percent of each mussel species collected during one- to two-hour searches at 28 reaches are summarized in Fig. 2. Three to six mussel species were usually observed at reaches nv02 through nv10 located in the lower and middle reaches of the basin. *Elliptio complanata* (Lightfoot 1786) was observed at 16 of 28 reaches and were the most widely distributed mussel species. Except for *Pyganodon*

*cataracta* (Say 1817), *Alasmidonta heterodon* and *Anodonta implicata* (Say 1829) were the most narrowly distributed species; they only were observed at reaches nv02 through nv05, downstream from the Cuddebackville Dam. One *P. cataracta* specimen was collected at reach ss01, immediately upstream of an abandoned beaver pond. *Alasmidonta varicosa*, *Strophitus undulatus* (Say 1817) and *Alasmidonta undulata* (Say 1817) were observed at 7-9 main-stem reaches in the low to middle reaches of the basin; *A. undulata* was also observed at two tributary reaches: tv01 and bk01 (Fig. 2).

Dense mussel beds of the main-stem Neversink River, were usually located outside the gorge and associated with several well-defined hydrologic and geomorphic settings. Mussel beds were often observed in shallow to moderately deep pools; however, they were most common in low to moderate-velocity glides at the downstream end (tail-out) of long pools which were controlled and stabilized by main-channel islands or bars. Beds of low-to-high mussel density were also found in moderate-velocity riffles and runs immediately downstream from these pool controls, but seldom where high-velocity rapids were evident. All mussel beds, regardless of geomorphic channel type, were generally denser along the channel margins than in the channel center. Small lateral pools located below gravel bars at the downstream end of short or long riffles and rapids sometimes contained high mussel densities. Substrate at reaches with dense mussel beds typically had low percent sand, fines, and embeddedness and high percent gravel and cobble. Large cobble and boulders were seldom evident in shallow runs and riffles where mussels were common. Individual mussels and sparse beds, however, were occasionally observed in moderately deep pools, riffles, or rapids where large cobble and (or) boulders created a matrix with fines, sand, and gravel-sized substrate and moderate-sized backwaters.

### *Mussel richness*

Richness of mussel communities decreased significantly with increasing elevation and distance from confluence (location) and increased with channel size and concentration of nutrients, cations and anions, and ANC (Table 2). Regression results (Table 3) indicate that physical, chemical, and spatial variables together explained as much as 84.5% of the variation in mussel-species richness. Individually, four physical variables, elevation, maximum depth, maximum depth of fines, and pool-riffle ratio, significantly explained 76.2 % of the variation. Three chemical variables, total phosphorus, ammonia, and pH, significantly explained 69.5% of the variation in richness. Two spatial variables, distance (location) and dam (orientation of each reach upstream or downstream of the Cuddebackville Dam) significantly explained 60.2% of the

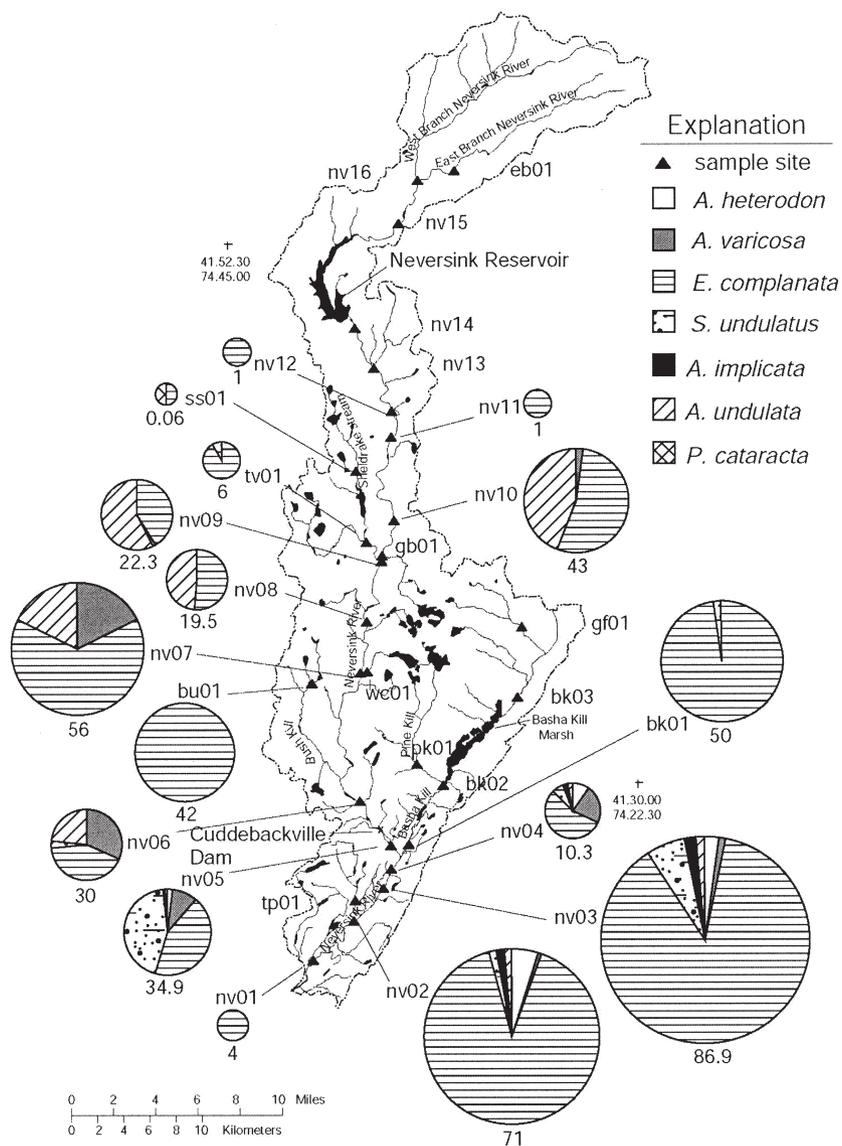


FIG. 2. Percent relative abundance of each mussel species (pie slices) and the total number of mussels collected per hour (under pies) at 28 sites in the Neversink River Basin, June - August, 1997; no mussels were observed at sites without pies.

variation. The variation explained by each of the three components add up to more than 100% due to shared variation (overlap) among variables that are spatially or multi-correlated.

Partial analyses indicate that pure physical habitat explained 11.1% of the variation, whereas, pure chemistry and space explained negative or small percentages of variation in mussel richness (Table 3). Pure environment (physical and chemical factors combined) explained 24.3 % of the variation. A large amount of the variation explained alone by either physical, chemical, or spatial components was actually overlap; *i.e.*, shared between (6.6 to 12.3%) and among 46.2% of the three components (Table 3, Fig. 3A). These findings show that there was spatial dependency among mussel, physical, and chemical variables. Though species richness was significantly related to both the location and the orientation of each reach upstream or downstream of the Cuddebackville Dam, pure location explained 29.6%, pure dam explained -3.6%, and 34.2% of the variation in species richness was shared between both factors (Table 4).

### *Mussel abundance*

The total number of mussels at each site, like richness, decreased at reaches further upstream, but was significantly correlated only with distance from confluence and ammonia concentrations (Table 2). Physical, chemical, and spatial variables together explained 50.8% of the variation in abundance of mussels (Table 3) at all but three reaches upstream from the Neversink Reservoir. The third physical-habitat principal component axis, (PPCA3) significantly explained 42.7% of the variation in abundance of mussel communities and represented a gradient in substrate type as well as stream order and elevation; percent gravel was negatively correlated, and maximum substrate size, elevation, and slope were positively correlated with PPCA3. Alone, three chemical variables, ammonia, potassium, and dissolved phosphorus, significantly explained 59.1% of the variation in total abundance. Alone, the spatial variables, dam and location, significantly explained 30.4% of the variation in mussel abundance (Table 4).

Partial analyses indicated that pure chemistry explained 8.5% of the variation, whereas, pure physical habitat and pure space only explained negative amounts of variation in total mussel abundance (Fig. 3B). Pure environment (physical and chemical factors combined) explained 20.4% of the total variation. The moderate amounts of explained variation shared between physical, chemical, and spatial variables (2.9 to 16.3%) and among all variables (27.9%) (Fig. 3B) indicate that there was spatial dependency. Considering spatial factors, location significantly explained 30.4% and the dam explained 17.4% of the variation in

TABLE 2. Significant Pearson coefficients of correlation ( $p \leq 0.10$ ) between richness of mussel communities, total abundance of all mussels, and relative abundance of each mussel species with physical, chemical, and spatial characters at 20 reaches in the Neversink River Basin, 1997-2001.

Predictor variable	Mussel-species richness	Abundance						
		All mussels	<i>Elliptio complanata</i>	<i>Strophitus undulatus</i>	<i>Alasmidonta undulata</i>	<i>Alasmidonta varicosa</i>	<i>Pyganodon heterodon implicata</i>	
Open canopy	-	-	-	-	0.59	-	-0.76	-0.78
Mean channel width	0.54	-	-	-	-	-	0.62	0.56
Max. channel width	0.51	-	-	-	-	-	0.67	0.69
Embeddedness	-	-	-	-	-	-0.58	-	-
Percent boulder	-	-	-	-	0.56	0.59	-	-
Percent cobble	-	-	0.64	-	-	-	-	-
Percent sand	-	-	-	-	-	-0.71	-	-
Mean substrate size	-	-	-	0.59	-	0.66	-	-
Depth of fines	-	-	-	-	-	-0.53	-	-
Percent algae	-0.45	-	-	-0.56	-	-	-	-
Vegetation index	-	-	-	-	-	0.71	-	-
Watershed area	0.51	-	-	-	-	-	0.67	0.65
Elevation	-0.70	-	-	-0.46	-	-	-0.60	-0.58
Mean annual flow	0.50	-	-	-	-	-	0.66	0.64
Channel slope	-	-	-	-	-	-0.76	-	-
Max. channel depth	-	-	-	-	-0.81	-	-	0.56
Depth-width ratio	-0.42	-	-	-	-	-	-	-
Bank stability index	-	-	0.49	-	0.45 <sup>6</sup>	0.53 <sup>6</sup>	-	-
Mean bank height	-	-	-0.51	-	-	-	-	-
Conductivity	0.69	-	-	-	-	-	-	-
Hardness	0.71	-	-	-	-	-	0.59	0.57
Calcium	0.71	-	-	-	-	-	0.65	0.64
Potassium	0.57	-	-	-	-	-	-	-
Sodium	0.72	-	-	-	-	-	-	-

(continued on next page)

TABLE 2 (continued)

Predictor variable	Mussel-species richness	Abundance						
		All mussels	<i>Elliptio complanata</i>	<i>Strophitus undulatus</i>	<i>Alasmidonta undulata</i>	<i>Alasmidonta varicosa</i>	<i>Pyganodon heterodon</i>	<i>Anodonta imbecilis</i>
ANC <sup>1</sup>	0.66	-	-	-	-	-	0.64	0.63
Chloride	0.70	-	-	-	-	-	-	-
Silica	0.46	-	-	-	-0.65	-	0.57	-
Sulfate	0.70	-	-	-	-	-	-	-
Ammonia	-	-0.69	-0.63	-	-	-	-	-
Total dissolved N <sup>2</sup>	-	-	-	-	-	0.63	-0.61	-0.68
Nitrate	-	-	-	-	0.57	0.66	-0.65	-0.69
Nitrite	0.52	-	-	-	0.88	-	-	-
Dissolved organic N	0.57	-	-	-	-	-	-	-
Total N	-	-	-	-	0.42	0.65	-0.64	-0.69
Ortho P <sup>3</sup>	0.71	-	-	-	0.67	0.72	-0.72	-0.74
Dissolved P	0.78	-	-	-	0.69	0.72	-0.65	-0.65
Total P	0.81	-	-	-	-	0.80	-	-
DOC <sup>4</sup>	0.42	-	-	-	-	-	-	-
Alim <sup>5</sup>	0.47	-	-	-	-	-	-	-
Dam	0.55	-	0.42	-	-0.63	-	0.79	0.76
Location	-0.80	-0.55	-0.68	-	-	-	-0.61	-0.60

<sup>1</sup> acid neutralizing capacity

<sup>2</sup> nitrogen

<sup>3</sup> phosphorus

<sup>4</sup> dissolved organic carbon

<sup>5</sup> Inorganic monomeric aluminum

<sup>6</sup> negatively correlated with erodibility

mussel abundance (Table 4). Location predicted abundance better than both variables combined, pure location explained 4%, and about a quarter of the variation was shared between dam and location.

### *Elliptio complanata*

*Elliptio complanata* was the most widely distributed and dominant mussel species at most reaches in the Neversink River Basin (Fig. 2). They comprised 74% of all mussels observed in the basin. Thus, it is unremarkable that the variables correlated to total abundance of all mussels were also correlated to abundance of *E. complanata* populations (Table 2). Abundance of *E. complanata* was significantly correlated with chemical-principal components axis 1 (CPCA1), physical-principal components axes 3 (PPCA3), the dam, and reach location. Physical, chemical, and spatial variables together could explain about 90% of the variation in the abundance of *E. complanata* populations (Table 3) at all except for three reaches above the Neversink Reservoir. Physical-PCA2 and PPCA3 significantly explained 60.0% of the variation in abundance of *E. complanata* populations. Physical-PCA3 represented a gradient in substrate as well as stream order/elevation as noted above for all mussels. Physical-PCA2 represented a gradient in channel size/depth; mean depth and width were positively correlated, and the bank stability index was negatively correlated, with PPCA2. Chemical-PCA1, potassium, dissolved phosphorus, and ammonia significantly explained 88.9% of the variation in *E. complanata* abundance. Conductivity, hardness, and concentration of cations and anions (Ca, Na, Cl, and SO<sub>4</sub>) were positively correlated with CPCA1. The spatial variables, dam and location, significantly explained 49.1% of the variation (Table 4).

Partial analyses indicate that pure chemistry explained 24.7% of the variation in *Elliptio complanata* populations and that physical-habitat and space only explained negative amounts of variation (Table 3, Fig. 3C). Pure environment (physical and chemical factors combined) explained 34.6% of the total variation. The large amount of explained variation shared between physical, chemical, and spatial variables (4.8-17.4%) and among all variables (42.0%) (Fig. 3C) indicate that there was spatial dependency. Considering only spatial factors, pure location explained 31.7%, pure dam explained 2.6%, and overlap explained 14.8% of the variation in *E. complanata* abundance (Table 4).

### *Strophitus undulatus*

*Strophitus undulatus* populations were most abundant just downstream from the Cuddebackville Dam and were the only species, other than *Elliptio*

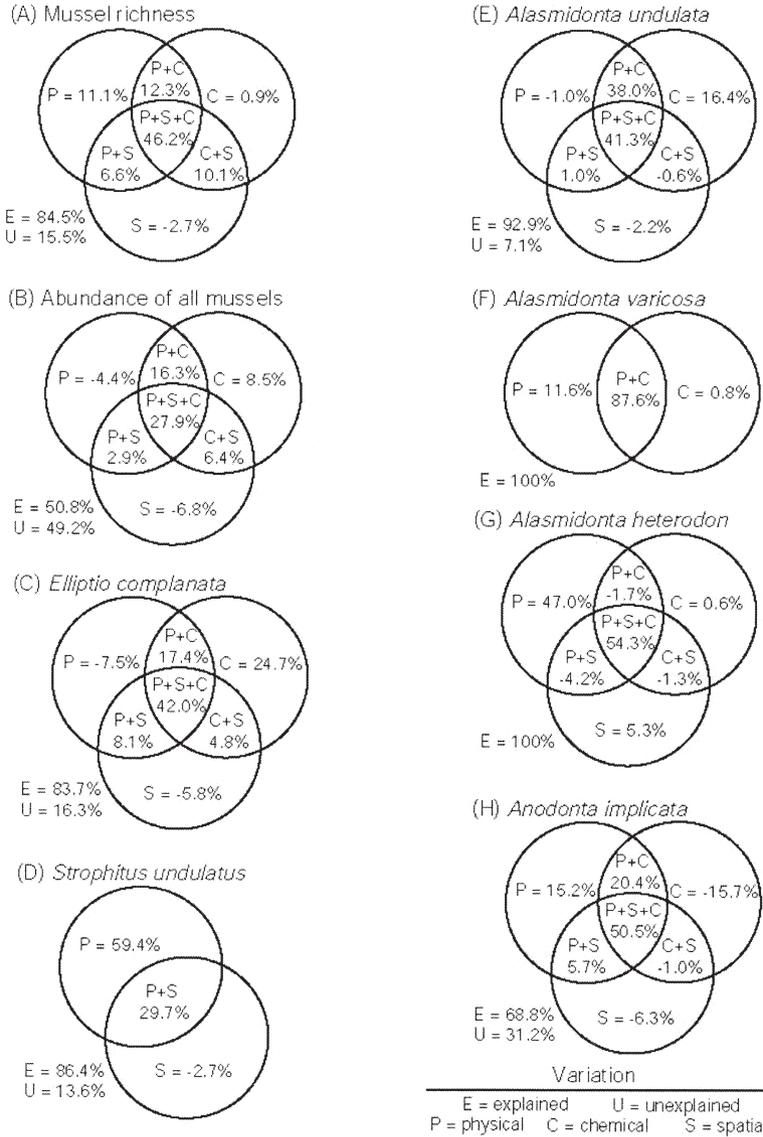


FIG. 3. Total amount of explained-E and unexplained-U variation in the (A) richness of mussel communities, abundance of (B) all mussels, and relative abundance of (C) *E. complanata*, (D) *S. undulatus*, (E) *A. undulata*, (F) *A. varicosa*, (G) *A. heterodon*, and (H) *A. implicata*. The percent of explained variation is partitioned into physical-P, chemical-C, and spatial-S components and into variation shared (overlap) between and among the three components. [Negative values are due to component calculations based on difference and are interpreted as approximately zero.]

TABLE 3. The cumulative variation in mussel species richness, abundance of all mussels, and relative abundance of each mussel species explained by physical, chemical, and spatial components; total variation explained (and unexplained) by combined variables; and pure variation attributed to each component and shared between and among the components. [Negative values are due to component calculations based on difference and are interpreted as approximately zero.]

Dependent variable	Cumulative variation explained by variables for each component			Cumulative variation associated with combined components			Variation in dependent variables explained by partitions					
	Physical	Chemical	Spatial	Explained (E)	Unexplained (U)	Physical (P)	Chemical (C)	Spatial (S)	Shared (P/C)	Shared (P/S)	Shared (C/S)	Shared (P/C/S)
Species richness:	76.2	69.5	60.2	84.5	15.5	11.1	0.9	-2.7	12.3	6.6	10.1	46.2
Abundance												
of all mussels	42.7	59.1	30.4	50.8	49.2	-4.4	8.5	-6.8	16.3	2.9	6.4	27.9
of <i>E. complanata</i>	60.0	88.9	49.1	83.7	16.3	-7.5	24.7	-5.8	17.4	8.1	4.8	42.0
of <i>S. undulatus</i>	89.1	ns <sup>1</sup>	27.0	86.4	13.6	59.4	0.0	-2.7	0.0	29.7	0.0	0.0
of <i>A. undulata</i>	79.3	95.1	39.5	92.9	7.1	-1.0	16.4	-2.2	38.0	1.0	-0.6	41.3
of <i>A. varicosa</i>	99.2	88.4	ns	100.0	0.0	11.6	0.8	0.0	87.6	0.0	0.0	0.0
of <i>A. heterodon</i>	95.4	51.9	54.1	100.0	0.0	47.0	0.6	5.3	-1.7	-4.2	-1.3	54.3
of <i>A. implicata</i>	91.8	54.2	48.9	68.8	31.2	15.2	-15.7	-6.3	20.4	5.7	-1.0	50.5

<sup>1</sup> not significant

TABLE 4. The cumulative variation in mussel species richness, abundance of all mussels, and relative abundance of each mussel species explained by either location/distance or a binary-dummy variable for orientation upstream or downstream from the Cuddebackville Dam; total variation explained (and unexplained) by combined spatial variables; and pure variation attributed to each, and shared among, both spatial variables. [Bold values identify significant,  $p < 0.01$ , correlations. Negative values are due to component calculations based on difference and are interpreted as approximately zero.]

Dependent variable	Cumulative variation explained by each spatial variable		Total variation explained by combined spatial variables		Variation in dependent variables explained by variable partitions		
	Dam	Location	Explained (E)	Unexplained (U)	Dam (D)	Location (L)	Shared (D/L)
Mussel richness:							
Abundance	<b>30.6</b>	<b>63.8</b>	60.2	39.8	-3.6	29.6	34.2
of all mussels	<b>17.4</b>	<b>30.4</b>	21.4	78.6	-9.0	4.0	26.4
of <i>E. complanata</i>	<b>17.4</b>	<b>46.5</b>	49.1	50.9	2.6	31.7	14.8
of <i>S. undulatus</i>	<b>27.0</b>	17.8	27.6	72.4	9.8	0.6	17.2
of <i>A. undulata</i>	<b>39.5</b>	15.5	34.1	65.9	18.6	-5.4	20.9
of <i>A. varicosa</i>	0.5	7.7	-2.3	102.3	-10.0	-2.8	10.5
of <i>A. heterodon</i>	<b>62.1</b>	<b>37.7</b>	54.1	45.9	16.4	-8.0	45.7
of <i>A. implicata</i>	<b>58.3</b>	<b>35.7</b>	48.9	51.1	13.2	-9.4	45.1

*complanata* and *Pyganodon cataracta*, observed in Neversink River tributaries (Fig. 2). Abundance of *S. undulatus* was positively correlated with percent cobble and the bank stability index and negatively correlated with elevation, bank height, and percent algae (Table 2). Physical-habitat and spatial variables together explained 86.4% of the variation in abundance of *S. undulatus* populations observed at eight reaches across the Neversink River Basin (Table 3). Chemical variables could not significantly explain any variation. Four physical-habitat variables, percent cobble substrate, elevation, percent algae, and percent gravel substrate, significantly explained 89.1% of the variation in abundance of *S. undulatus* populations. The Cuddebackville Dam significantly explained 27.0% of variation (Table 3).

Partial regression analyses indicate that pure physical habitat explained 59.4% and pure space explained no variation in abundance of *Strophitus undulatus* populations; 29.7% of the explained variation was shared between the two components (Table 3, Fig. 3D). Only the Cuddebackville Dam was significantly related to *S. undulatus* abundance; pure dam explained 9.8%, pure location explained 0.6%, and overlap explained 17.2% of the variation in abundance of their populations (Table 4).

#### *Alasmidonta undulata*

The trend in abundance of *Alasmidonta undulata* populations in the Neversink River was the reverse of that observed for most other species. Abundance increased between lower- and middle-basin reaches and was very low downstream from the Cuddebackville Dam (Fig. 2). Densities were low at reaches downstream from the Cuddebackville Dam and generally increased at main stem reaches located further upstream until nv11, where no *A. undulata* were collected. Abundance was positively correlated with substrate size, bank stability, percent open canopy, and concentrations of most nutrients and negatively correlated with maximum channel depth and concentration of silica (Table 2). Physical, chemical, and spatial variables together explained 92.9% of the variation in abundance of *A. undulata* populations (Table 3). Maximum depth and bank stability significantly explained 79.3% of the variation in abundance of *A. undulata*. Dissolved P, sulfate, and ammonia significantly explained 95.1% of the variation in *A. undulata* populations. Like *Strophitus undulatus*, the dam was the only spatial factor that significantly explained variation (39.5%) in abundance of *A. undulata*.

Partial analyses indicate that pure chemistry explained 16.4% and pure physical habitat and space explained no variation in abundance of *Alasmidonta undulata* populations; 79.7% of the explained variation was shared among the

three components (Fig. 3E). Pure environment (physical and chemical factors combined) explained 53.4% of the total variation. Considering only spatial variables, pure dam explained 18.6% and overlap between the dam and location explained 20.9% of the variation in *A. undulata* abundance (Table 4). The large amount of variation shared between physical and chemical variables (38.0%) and among the three components (41.3%) indicate that there was spatial dependency among variables and that the Cuddebackville Dam affected abundance of *A. undulata* populations.

#### *Alasmidonta varicosa*

*Alasmidonta varicosa* were widely distributed across the Neversink River Basin and most abundant in mid-basin reaches near the Cuddebackville Dam; population abundance decreased at reaches located further upstream or downstream from the dam (Fig. 1). Abundance was positively correlated with the vegetation index, percent boulder, mean substrate size, bank stability, and nutrient concentrations and it was negatively correlated with the channel slope, embeddedness, depth of fines, and percent sand (Table 2). Physical-habitat and chemical variables together explained 100% of the variation in abundance of *A. varicosa* populations (Table 3). Spatial variables could not significantly explain any variation. Three physical variables, PPCA1, the vegetation index, and percent open canopy explained 99.2% of the variation in *A. varicosa* populations. Physical-PCA1 represented a gradient in stream size and substrate type; percent sand, embeddedness, pool-riffle ratio, and the depth-width ratio were negatively correlated, and drainage area and water velocity were positively correlated with PPCA1. Elevation, stream slope, and maximum depth also were good predictors of *A. varicosa* abundance in multiple regressions. Two chemical variables, total phosphorus and silica, significantly explained 88.4% of variation in their populations (Table 3).

Results of partial regression analyses indicate that pure physical-habitat explained 11.6% of the variation, and pure chemistry explained 0.8% of variation in abundance of *Alasmidonta varicosa* populations; 87.6% of the explained variation was shared between the two components (Table 3, Fig. 3F). The Cuddebackville Dam and location were not significantly related to abundance of *A. varicosa* populations (Table 4).

#### *Alasmidonta heterodon*

*Alasmidonta heterodon* (and *Anodonta implicata*) populations were only observed in main stem reaches downstream from the Cuddebackville Dam.

Abundance of *A. heterodon* populations in the basin were significantly and positively correlated with channel size (mean annual flow, channel width, drainage area), and to concentrations of hardness, Ca, silica, ANC and negatively correlated with elevation, percent open canopy, and concentrations of all nutrients (Table 2). Physical-habitat, chemical, and spatial variables together could explain 100% of the variation in abundance of *A. heterodon* populations (Table 3). Regression results based on variations in abundance of *A. heterodon* populations (and *A. implicata* below) at four reaches and on their absences at several nearby reaches are presented chiefly for empirical purposes. Physical-habitat variables, PPCA3, PPCA7, and mean bank height explained 95.4% of the variation in abundance of *A. heterodon* populations (Table 3). PPCA3 represented a gradient in substrate as well as stream order/elevation (percent gravel, maximum substrate size, elevation, and slope were highly correlated with PPCA3) as noted above for total number of mussels. PPCA7 represented a gradient in bank conditions and substrate size; mean bank width and percent open canopy were positively correlated, and the maximum particle size was negatively correlated with PPCA7. One chemical variable, orthophosphorus (ortho P) significantly explained as much as 51.9% of the variation (Table 3). The location and the Cuddebackville Dam significantly explained 54.1% of variation in their populations.

Partial regression analyses indicate that pure physical-habitat explained 47.0%, pure chemistry explained 0.6%, and pure space explained 5.3% of the variation in *Alasmidonta heterodon* populations (Table 3, Fig. 3G). Pure environment (physical and chemical factors combined) explained 45.9% of the total variation. Roughly, 47.1% of the explained variation was shared among all three components. Though the Cuddebackville Dam and location were both significantly related to *A. heterodon* abundance (Table 4), pure dam explained 16.4%, pure location explained 8%, and overlap explained 45.7% of the variation in abundance of their populations. Findings suggest there was spatial dependency among variables and that the Cuddebackville Dam affected abundance of *A. heterodon* populations.

### *Anodonta implicata*

The distribution of *Anodonta implicata* in the Neversink River was similar to that of *Alasmidonta heterodon* (Fig. 2), thus, it was not surprising that abundance was significantly correlated with most of the same variables (Table 2). Combined physical-habitat, chemical, and spatial variables, however, only explained 68.8% of the variation in abundance of their populations (Table 3). Three physical variables, PPCA3, percent cobble substrate, and bank stability,

significantly explained 91.8% of the variation in abundance. Physial-PCA3 represented a gradient in substrate type as well as stream order and elevation as noted above for abundance of all mussels. Ortho P significantly explained 54.2% of the variation. The location and the Cuddebackville Dam significantly explained 48.9% of variation in their populations.

Partial analyses (Fig. 3H) indicate that about 75% of the explained variation in *Anodonta implicata* populations was shared among physical, chemical, and spatial components. Pure physical-habitat explained 15.2% and pure chemistry and space explained negative amounts of variation. Pure environment (physical and chemical factors combined) explained 19.9% of the total variation. Like *Alasmidonta heterodon*, the Cuddebackville Dam and location were both significantly related to abundance of *A. implicata* (Table 4); however, pure dam explained 13.2%, pure location explained -9.4%, and overlap explained 45.1% of the variation in abundance. High levels of variation shared among all components (Fig. 3H) and the pure spatial variation attributed to the dam (Table 4) suggest that the Cuddebackville Dam affected the distribution and abundance of *A. implicata* populations.

## DISCUSSION

### *Mussel communities*

Abundance of mussel populations and, thus, species distributions and richness of mussel communities in the Neversink River Basin appear to be affected to different degrees by water-quality, habitat, spatial location (distance from mouth and proximity to other reaches), and the Cuddebackville Dam. Strong correlations among dependent and predictor variables imply that various factors may limit or regulate mussel populations or communities in the basin. Direct cause-and-effect relations, however, cannot be confirmed and mechanisms remain speculative because all findings are based on observations of natural ecosystems. Community richness, though moderately related to water quality, location, and the Cuddebackville Dam, was strongly related to several physical-habitat features. Total community abundance was related primarily to chemical factors and spatial location. Several investigations identified relations between the richness of mussel communities and microhabitat factors, landscape characteristics, and physiographic factors, but few noted strong relations between macrohabitat factors and the richness of mussel species or the distribution of individual species populations (Layzer & Madison, 1995; Strayer, 1993; Strayer, 1999; Strayer & Ralley, 1993; Vannote & Minshall, 1982). Stream size was the only macrohabitat variable significantly related

to mussel species richness in non-tidal streams of the northern Atlantic Slope (Strayer, 1993). The distribution of mussel species in the Salmon River, Idaho, was partly regulated by sediment stability (Vannote & Minshall, 1982). Similarly, the patchy distribution of mussel beds under favorable or marginal environmental conditions in the Neversink River was hypothesized to result from the stability of stream sediments during high flows (Strayer & Ralley, 1991). A recent study in the lower Neversink Basin showed that mussel-sized stones remain in mussel beds after large storm-flows and over periods of several years, whereas those at adjacent reaches (within meters) containing no mussels were buried or transported downstream (Strayer, 1999). Others have found that seemingly important factors, such as calcium concentration and stream size, were not good predictors of unionid richness (Strayer & Ralley, 1991), and depth, organic content and granulometry of sediment, distance from shore, and concentration of particulate organic matter in freshwater tidal environments did not explain species distributions or variability in abundance of five mussel species (Strayer *et al.*, 1994). Related studies have shown that water depth and velocity were correlated with the distribution of mussel species at base flows, and that shear stresses at low and moderate flows during the period of juvenile settlement were significantly correlated with mussel abundances at reaches along a 4th-order stream in the Cumberland River Basin, KY (Layzer & Madison, 1995). Shear stress, water velocity, stream discharge, and certain substrate particle sizes also had been shown or hypothesized to restrict mussel species to stable patches (microhabitats) in suitable reaches (Strayer *et al.*, 1994; Strayer, 1993; Strayer & Ralley, 1993). The findings from the present study and others suggest that reach conditions at moderate to high flow might govern the distribution of mussel species and the richness of mussel communities in lotic systems.

The inability of many studies to identify strong relations between predictor variables and mussel populations and communities may be due to a number of factors. First, the micro- and macro-habitat or biological factors that truly affect mussel assemblages may not have been adequately characterized. This is understandable considering several potential predictors, such as water depth, velocity, and bed shear stress at effective discharge, occur under difficult-to-measure high flow conditions in large streams and rivers. Other critical factors, such as the distribution of host-fish species, are seldom evaluated. For example, more than 50% of the variation in the mussel species assemblages at 36 reaches across the Red River drainage basin of Texas was explained, in part, by the distribution and abundance of native fish species (Vaughn & Taylor, 2000). Fish assemblages, pure space, and pure environment explained 15.4, 16.1, and 7.8 percent of the variation in the mussel-species matrix, respectively; overlap

among the three categories explained 40% of the variation (Vaughn & Taylor, 2000). More important, however, is the likelihood that individual mussel species are affected to different degrees by the same and different environmental factors. Various responses of different species across physical, chemical, and biological gradients in riverine systems can complicate community changes and confound or weaken evident relations. The effects that different environmental factors have on mussel communities can be refined after their effects on individual species populations are defined.

### *Mussel populations*

Though spatial structure (location) and physical-habitat affected abundance of *Elliptio complanata*, water quality appeared to be mainly responsible for regulating their populations in the Neversink River Basin. The absence of strong relations with physical-habitat features and the Cuddebackville Dam is not notable given their broad tolerance to environmental conditions; the species occurs under lotic and lentic conditions ranging from small brooks to large rivers and lakes (Strayer & Ralley, 1991). It is also one of the most widespread unionid species in New York State and often dominates mussel communities where they occur (Strayer & Ralley, 1991). Combined with the wide distribution and high abundance of *E. complanata* throughout the Neversink Basin, our findings support relations (or lack of relations) identified in several other studies. The presence of *E. complanata* was only weakly correlated to stream size, and the species was categorized, along with *Alasmidonta undulata* and *Strophitus undulatus*, as a generalist, having no strong relations with a number of macrohabitat factors in streams of the northern Atlantic Slope (Strayer, 1993). Poor habitat relations are exemplified by the decreases in *E. complanata* abundance associated with increasing distance from the mouth and decreasing ionic strength of stream waters at main-stem and tributary reaches, regardless of stream or channel width or depth, substrate characteristics, mean annual flow, or elevation. Its distribution in the Neversink suggests it prefers sites with low concentrations of nitrate, ammonia, and ammonium, but moderate to high concentrations of phosphorus, conductivity, hardness, K, Ca, Na, Cl, and sulfate; and that the species may tolerate waters with relatively high temperatures and low dissolved oxygen concentrations.

Abundance of *Strophitus undulatus* populations in the Neversink River was primarily affected by physical-habitat factors and possibly by the Cuddebackville Dam; water quality and location had little or no effect. The species is sometimes common in small streams and rivers across parts of New York State (Strayer & Ralley, 1991). Though *S. undulatus* was categorized as having few strong

preferences, its presence was weakly correlated with hydrologic stability and the lack of tidal influence in streams of the northern Atlantic Slope (Strayer, 1993). Its distribution in the middle and lower reaches of the Neversink support observations that stream size and hydrologic stability could regulate their populations. They were typically more abundant at sites downstream of nv06 (the first reach above the Cuddebackville Dam) than above, and abundance was positively related to percent cobble and gravel substrate and bank stability and negatively related to bank height and elevation. The presence of *S. undulatus* both upstream and downstream from the Cuddebackville Dam indicate the dam does not strongly affect population abundance, and that it is not a barrier to dispersion of the species.

Physical habitat, water quality, location, and the Cuddebackville Dam were all related to abundance of *Alasmidonta undulata* populations in the Neversink River; however, chemical factors appeared to be most important. Increasing densities at reaches further upstream was the reverse of trends for most other mussel species, but support the view that the species prefers large streams and small rivers (Strayer & Jirka, 1997; Strayer & Ralley, 1991). Though few other studies report preferences, the presence of *A. undulata* populations was weakly correlated with hydrologic stability, low Ca concentration, and the lack of tidal influence in streams of the northern Atlantic Slope (Strayer, 1993). Distribution of *A. undulata* and water quality data from the Neversink Basin suggest they prefer relatively high nutrient and productivity levels and low to intermediate concentrations of cations and anions, hardness, silica, sulfate, and ANC. These conditions occur at reaches with intermediate elevations, drainage areas, stream size, flows, temperatures, and hydrologic stability and may be the basis for large amounts of explained variation being shared among chemical, physical and spatial components. High levels of shared variation, coupled with pure variation, explained by the Cuddebackville Dam indicate that reach location and orientation to the Cuddebackville Dam affected abundance of *A. undulata* populations in the basin. Unlike populations of *Alasmidonta heterodon* and *Anodonta implicata* (see below), the dam appeared to separate larger populations in the middle reaches from smaller populations in the lower reaches. If not a result of unsuitable environmental conditions, low densities below the dam could be due to host fish species that are confined mainly to the middle basin or to heightened inter- and intra-specific competition with other mussel species, such as *A. heterodon* and *A. implicata*, which only occur downstream of the Cuddebackville Dam.

Abundance and distributions of *Alasmidonta varicosa* populations in the Neversink River were affected mainly by physical-habitat factors and to a lesser extent by water-quality conditions; they were not affected by spatial location

or by the Cuddebackville Dam. *Alasmidonta varicosa* populations in the Neversink River were most abundant at mid-basin reaches where channel slope (0.70-0.75%) and percent boulder substrate (28-44%) were high and percent sand (19%) and embeddedness (20%) were at or near their minimums. At these reaches, median concentrations of Ca were about 5.0 mg/L, hardness was 17-18 mgCaCO<sub>3</sub>/L, and total phosphorus (P) was about 0.050 mg/L. Species abundance was lower at reaches where concentrations of the three constituents were higher or lower. These results support findings from several other studies. Strayer & Jirka (1997) report that *A. varicosa* typically favor gravelly riffles in small rivers and streams that are nutrient poor and have low calcium concentrations. In a study of microhabitat preferences in the Neversink River, *A. varicosa* were found most frequently in quadrants with moderate velocities, with a high proportion of medium sands (0.25-1.0 mm), and intermediate depths (Strayer & Ralley, 1993). The presence of *A. varicosa* was strongly and negatively correlated only with Ca concentration in an evaluation of mussel-macrohabitat relations in streams of the northern Atlantic Slope (Strayer, 1993).

The presence of *Alasmidonta varicosa* at reaches above and below the Cuddebackville Dam and the absence of *Alasmidonta heterodon* above the dam are somewhat perplexing because both mussel species use closely related fish species as hosts (Strayer & Jirka, 1997). At least two resident fish species, the longnose dace, *Rhinichthys atratulus* (Hermann, 1804), and the slimy sculpin, *Cottus cognatus* (Richardson, 1836), are known hosts for *A. varicosa*, and the mottled sculpin, *Cottus bairdi* (Girard 1850), is a known host for *A. heterodon* (Strayer & Jirka, 1997). Presumably, either *A. varicosa* were present upstream of the Cuddebackville Dam before the early 1800s when the dam was first built, or one host fish species specific to *A. varicosa* can negotiate the dam's low head. In either case, the low head dam has little effect on the distribution of their populations.

Though physical-habitat variables alone could explain most of the variation in abundance of *Alasmidonta heterodon* populations in the Neversink River, the high amount of variation shared among physical, chemical, and spatial components suggests the species may be affected by many factors, including the Cuddebackville Dam and spatial location, elevation, percent open canopy, percent gravel, slope, maximum substrate size, concentration of nutrients. While few strong physical-habitat or chemical preferences are known for the species (Strayer & Ralley, 1993), findings from this study and those from several others suggest that the distribution and abundance of *A. heterodon* may be governed primarily by certain substrate matrices, channel sizes and depths, water velocities, and water-quality conditions. In laboratory experiments, individual *A. heterodon* specimens did not distinguish between moving or static

waters but they always preferred finer vs. coarser substrates (Michaelson & Neves, 1995). In studies of microhabitat preferences in the Neversink River, *A. heterodon* were most frequently observed in quadrants with uniform and moderate velocities, intermediate depths, and with finer sediment patches that accumulate between cobbles (Strayer & Ralley, 1993). On a larger scale (1 to 10 km), *A. heterodon* abundance in streams of the northern Atlantic Slope were negatively correlated to calcium concentration and stream gradient (Strayer, 1993).

Negative relations with nutrients indicate that enrichment in middle and upper reaches of the Neversink could pose a threat to downstream populations of *Alasmidonta heterodon* and to the possible expansion of their populations into middle reaches of the basin. Limited water-quality preferences were indicated for *A. heterodon* as it was only found at reaches where median concentrations of nitrate were less than 0.4 mg N/L, ortho P was less than 0.030 mgP/L, and total phosphorus was less than 0.055 mgP/L. Residential septic systems across the basin, runoff of residential and agricultural fertilizers and municipal sewage-treatment effluents in the middle basin (TNC, 1999), and deposition of nitrous oxides in the poorly-buffered headwater reaches (Baldigo & Lawrence, 2000, Lawrence *et al.*, 1999; Lawrence *et al.*, 2000) are known or potential sources of eutrophication in the watershed.

The empirical relations defined above need to be qualified because any effects that the Cuddebackville Dam has on the distribution of *Alasmidonta heterodon* in the basin would partly nullify identified associations. Partial regression analyses indicate that distribution of *A. heterodon* in the Neversink River could have been affected by the Cuddebackville Dam. The low-head dam could physically limit expansion of *A. heterodon* populations because it blocks upstream movement of the tessellated darter, *Etheostoma olmstedi* (Storer 1842), which is a known host for the glochidea (larval) life stages of the dwarf wedgemussel (Michaelson & Neves, 1995). If part or all of the Cuddebackville Dam were removed to allow passage for this species and for anadromous fish that also are potential hosts (see *Anodonta implicata* below), then expansion of *A. heterodon* populations would be plausible. If the dam does restrict *A. heterodon* populations, identified relations might be biased and would need to be redefined if the species populated additional reaches.

The distribution of *Anodonta implicata* populations in the Neversink River match that of *Alasmidonta heterodon*; thus, it not surprising that their abundances were affected by most of the same factors. The presence of *A. implicata* in the Neversink River was a little unexpected as it is most commonly found in large rivers just upstream of the head of the tide (Strayer, 1993). In streams of the northern Atlantic Slope, *A. implicata* populations were strongly

correlated with tidal influence, Ca concentration, hydrologic stability, and gradient (Strayer, 1993). Though environmental preferences for the species are not known, positive correlations of abundance with annual discharge, channel width, drainage area, Ca, and ANC and negative correlations with nutrient concentrations in the Neversink suggest the species can prosper in high order, low elevation, and deep rivers with relatively warm and moderate-velocity waters. Conditions suitable for *A. implicata* in the Neversink River were comparable to those in the Hudson and Connecticut River Basins where the species was also observed (Strayer & Jirka, 1997).

Like *Alasmidonta heterodon*, the Cuddebackville Dam appears to restrict *Anodonta implicata* populations to lower reaches of the Neversink River Basin. There is strong circumstantial evidence that obstacles to migration for a known host fish species could restrict *A. implicata* populations in the Neversink River. The upstream extent of *A. implicata* populations was increased in the Connecticut River following implementation of a shad-restoration program that included removal of at least one dam (Smith, 1985). The Cuddebackville Dam currently blocks upstream migration of anadromous American shad (*Alosa sapidissima* Wilson 1811) and hickory shad (*Alosa mediocris* Mitchell 1814) (TNC, 1999), at least one of which is a host for glochidea of *A. implicata* (Strayer & Jirka, 1997). Expansion of *A. implicata* (and *A. heterodon*) populations into middle reaches of the Neversink, like that observed in the Connecticut River, may be possible after the Cuddebackville Dam is removed.

Little can be inferred about the factors that might affect *Pyganodon cataracta* populations in the Neversink Basin because they were only found in one small tributary upstream from an abandoned beaver pond. Their absence from all riverine reaches in the Neversink could have been predicted because the species is usually encountered in quiet, well-protected ponds, and marshes (Strayer & Jirka, 1997).

#### *Potential effects of the Neversink Reservoir on mussel communities*

The present study determined that the Cuddebackville Dam could potentially affect the distribution of two or three mussel species in the lower Neversink River Basin. Effects of the Neversink Reservoir on mussel distributions could potentially be more significant due to impacts on downstream water quality and hydrologic regime. Possible effects of the reservoir, like that of the Cuddebackville Dam, are also speculative because no pre-construction mussel data are available to evaluate changes. Dams not only block fish migration and alter downstream riverine habitat, they significantly change water-temperature regimes, alter water quality, alter normal thermal and hydrologic regimes, and

increase hydrologic and sediment stability (Anonymous, 1997; Richter *et al.*, 1997a). These alterations modify the distribution and availability of riverine habitat and disrupt native biodiversity and ecological integrity of affected reaches (Poff *et al.*, 1997; Richter *et al.*, 1996; Richter *et al.*, 1997b). Annual peak flows at a USGS continuous-discharge gage immediately downstream from the Neversink Reservoir (site nv14) decreased, on average, from 310 to 150 m<sup>3</sup>/s after completion of the dam. These changes increased hydrologic and channel stability and decreased bed-sediment loads. The loss of seasonal flow peaks and changes to the timing of annual maximum and minimum flows in the Neversink River likely affected aquatic species that use flow cues for spawning, migration, and egg hatching; the distribution of native fish and macroinvertebrate species; and the composition of affected communities. Dampened discharge peaks and increased substrate stability could have been favorable to the establishment and long-term maintenance of mussel beds. The possibility that both main stem impoundments in the basin could have beneficial as well as adverse effects on populations of common, threatened, and endangered mussels has broad implications for watershed and reservoir management and for ecosystem restoration. Some semblance of original biodiversity and ecosystem integrity might be reconstituted in the Neversink and in similar regulated rivers if water releases from reservoirs were managed to approximate certain components of natural flow regimes. In an era of stream and ecosystem restoration, both the negative effects and the positive management potential of impoundments need to be evaluated before plans to restore natural biodiversity and hydrogeomorphology in riverine systems are implemented.

#### ACKNOWLEDGEMENTS

We wish to thank the O'Connell Foundation, which partly funded this study. We also extend thanks to the Town of Thompson and Anthony Cellini for project support, Orange County Department of Parks, Recreation, and Conservation and the many landowners in the basin that permitted access to the Neversink River through their properties, and Colin Apse, Alton Anderson, Gretchen Wall, Dave R. Smith, and Dave L. Strayer for technical assistance.

#### LITERATURE CITED

- Anonymous. 1997. Effects of dams on downstream resources explored. *Fisheries*, 22: 46-47.
- BALDIGO, B.P. & G.B. LAWRENCE. 2000. Composition of fish communities in relation to stream acidification and habitat in the Neversink River, New York. *Transactions of the American Fisheries Society*, 129: 60-76.
- BOGAN, A.E. 1993. Freshwater bivalve extinctions (Mollusca: Unionidae): a search for causes. *American Zoologist*, 33: 599-609.
- BRIM-BOX, J. & J. MOSSA. 1999. Sediment, land use, and freshwater mussels: prospects and problems. *Journal of the North American Benthological Society*, 18: 99-117.

- BUTCH, G.K., R. LUMIA & P.M. MURRAY. 1998. Water Resources Data New York — Water Year 1997 Volume 1. Eastern New York excluding Long Island. Pp. 252-260. U.S. Geological Survey, Troy, NY. 350 pp.
- FISHMAN, M.J. & L.C. FRIEDMAN. 1989. *Methods for the determination of inorganic substances in water and fluvial sediments: U.S. Geological Survey Techniques of Water-Resources Investigations Book 5, Chapter A1*. Pp. 111-145. U.S. Department of Interior, Denver, CO. 545 pp.
- FRISSELL, C., W. LISS, C. WARREN & M. HURLEY. 1986. A hierarchical framework for stream habitat classification - Viewing streams in a watershed context. *Environmental Management*, 10: 199-214.
- KREJMAS, B.E., W.E. HARKNESS, W.J. CARSWELL, Jr. & H.L. DARLING. 1998. Report of The River Master of the Delaware River For the Period December 1, 1997 - November 30, 1998. Pp. 24-27. U.S. Geological Survey, Milford, PA. 93 pp.
- LAWRENCE, G., T. LINCOLN, D. HORAN-ROSS, M. OLSON & L. WALDRON. 1995. Analytical Methods of the U.S. Geological Survey's New York District Water-Analysis Laboratory. Pp. 7-60. U.S. Geological Survey, Troy, NY. 78 pp.
- LAWRENCE, G.B., M.B. DAVID, G.M. LOVETT, P.S. MURDOCH, D.A. BURNS, J.L. STODDARD, B.P. BALDIGO, J.H. PORTER & A.W. THOMPSON. 1999. Soil calcium status and the response of stream chemistry to changing acid deposition rates. *Ecological Applications*, 9: 1059-1072.
- LAWRENCE, G.B., G.M. LOVETT & Y.H. BAEVSKY. 2000. Atmospheric deposition and watershed nitrogen export along an elevational gradient in the Catskill Mountains, New York. *Biogeochemistry*, 50: 21-43.
- LAYZER, J.B. & L.M. MADISON. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Regulated Rivers: Research & Management*, 10: 329-345.
- LEGENDRE, P. & L. LEGENDRE. 1998. *Numerical ecology, Second English edition*. Pp. 497-545. Elsevier, Oxford. 853 pp.
- MASTER, L.L. 1990. The imperiled status of North American aquatic animals. *Biodiversity Network News*, 3: 1-8.
- MEADOR, M., C. HUPP, T. CUFFNEY & M. GURTZ. 1993. Methods for characterizing stream habitat as part of the National Water-Quality Assessment Program. Pp. 6-40. U.S. Geological Survey. 48 pp.
- METCALFE-SMITH, J.L., J. Di MAIO, S.K. STANTON & G.L. MACKIE. 2000. Effect of sampling effort on the efficiency of the timed search methods for sampling freshwater mussel communities. *Journal of the North American Benthological Society*, 19: 725-732.
- MICHAELSON, D.L. & R.J. NEVES. 1995. Life history and habitat of the endangered dwarf wedgemussel *Alasmidonta heterodon* (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, 14: 324-340.
- PLATTS, W., W. MEGAHAN & G. MINSHALL. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service, Ogden, Utah. 70 pp.
- POFF, N.L., J.D. ALLAN, M.B. BAIN, J.R. KARR, K.L. PRESTEGAARD, B.D. RICHTER, R.E. SPARKS & J.C. STROMBERG. 1997. The natural flow regime: a paradigm for river conservation and restoration. *Bioscience*, 47: 769-784.
- RANTZ, S.E. 1983. Measurement and computation of streamflow—v. 1, Measurement of stage and discharge. Pp. 79-183. U. S. Geological Survey. 284 pp.
- RICHTER, B.D., J.V. BAUMGARTNER, D.P. BRAUN, & J. POWELL. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, 10: 1163-1174.
- RICHTER, B.D., J.V. BAUMGARTNER, R. WIGINGTON & D.P. BRAUN. 1997b. How much water does a river need? *Freshwater Biology*, 37: 231-249.

- RICHTER, B.D., D.P. BRAUN, M.A. MWDELSON & L.L. MASTER. 1997a. Threats to imperiled freshwater fauna. *Conservation Biology*, 11: 1081-1093.
- SIMONSON, T.D., J. LYONS & P.D. KANEHL. 1993. Guidelines for evaluating fish habitat in Wisconsin streams. Pp. 4-30. U.S. Forest Service, St. Paul, MN. 36 pp.
- SIMONSON, T.D., J. LYONS & P.D. KANEHL. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. *North American Journal of Fisheries Management*, 14: 607-615.
- SMITH, D.G. 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River system. *Freshwater Invertebrate Biology*, 4: 105-108.
- STRAYER, D.L. 1993. Macrohabitats of freshwater mussels (Bivalvia: Unionacea) in streams of the northern Atlantic Slope. *Journal of the North American Benthological Society* 12: 236-246.
- STRAYER, D.L. 1999. Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society*, 18: 468-476.
- STRAYER, D.L., D.C. HUNTER, L.C. SMITH & C.K. BORG. 1994. Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. *Freshwater Biology*, 31: 239-248.
- STRAYER, D.L. & K.J. JIRKA. 1997. *The pearly mussels of New York State*. Pp. 43-87. The University of the State of New York, Albany, NY. 113 pp.
- STRAYER, D.L., S.E. MAY, P. NIELSON, W. WOLLHEIM & S. HAUSAM. 1997. Oxygen, organic matter, and sediment granulometry as controls on hyporheic animal communities. *Archiv für Hydrobiologie*, 140: 131-144.
- STRAYER, D.L. & J. RALLEY. 1991. The freshwater mussels (Bivalvia: Unionidea) of the upper Delaware River drainage. *American Malacological Bulletin*, 9: 21-25.
- STRAYER, D.L. & J. RALLEY. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society*, 12: 247-258.
- STRAYER, D.L., S.J. SPRAGUE & S. CLAYPOOL. 1996. A range-wide assessment of populations of *Alasmidonta heterodon*, an endangered freshwater mussel (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, 15: 308-317.
- TNC (The Nature Conservancy). 1995. Neversink River Bioserve Strategic Plan. Pp. 4-25. The Nature Conservancy Lower Hudson Chapter, Mount Kisco, NY. 46 pp.
- TNC (The Nature Conservancy). 1999. Neversink River Site Conservation Plan: Vision, Target and Strategy Update for 1999-2002. Pp. 8-47. The Nature Conservancy Lower Hudson Chapter, Mount Kisco, NY. 53 pp.
- VANNOTE, R.L. & G.W. MINSHALL. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Sciences*, 79: 4103-4107.
- VAUGHN, C.C. & C.M. TAYLOR. 1999. Impoundments and the decline of freshwater mussels: A case study of an extinction gradient. *Conservation Biology* 13: 912-920.
- VAUGHN, C.C. & C. M. TAYLOR. 2000. Macroecology of a host-parasite relationship. *ECOGRAPHY*, 23, 11-20.
- WILLIAMS, J.D. & R.J. NEVES. 1995. Freshwater mussels: a neglected and declining aquatic resource. Pp. 19-21, in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran & M.J. Mac (eds.). *Our living resources: a report to the nation on the abundance, and health of U.S. plants, animals, and ecosystems*. U.S. Department of Interior, National Biological Service, Washington, D.C. 530 pp.
- WOLMAN, M. 1954. A method for sampling coarse river-bed material. *Transactions of the American Geophysical Union*, 235: 951-956.